

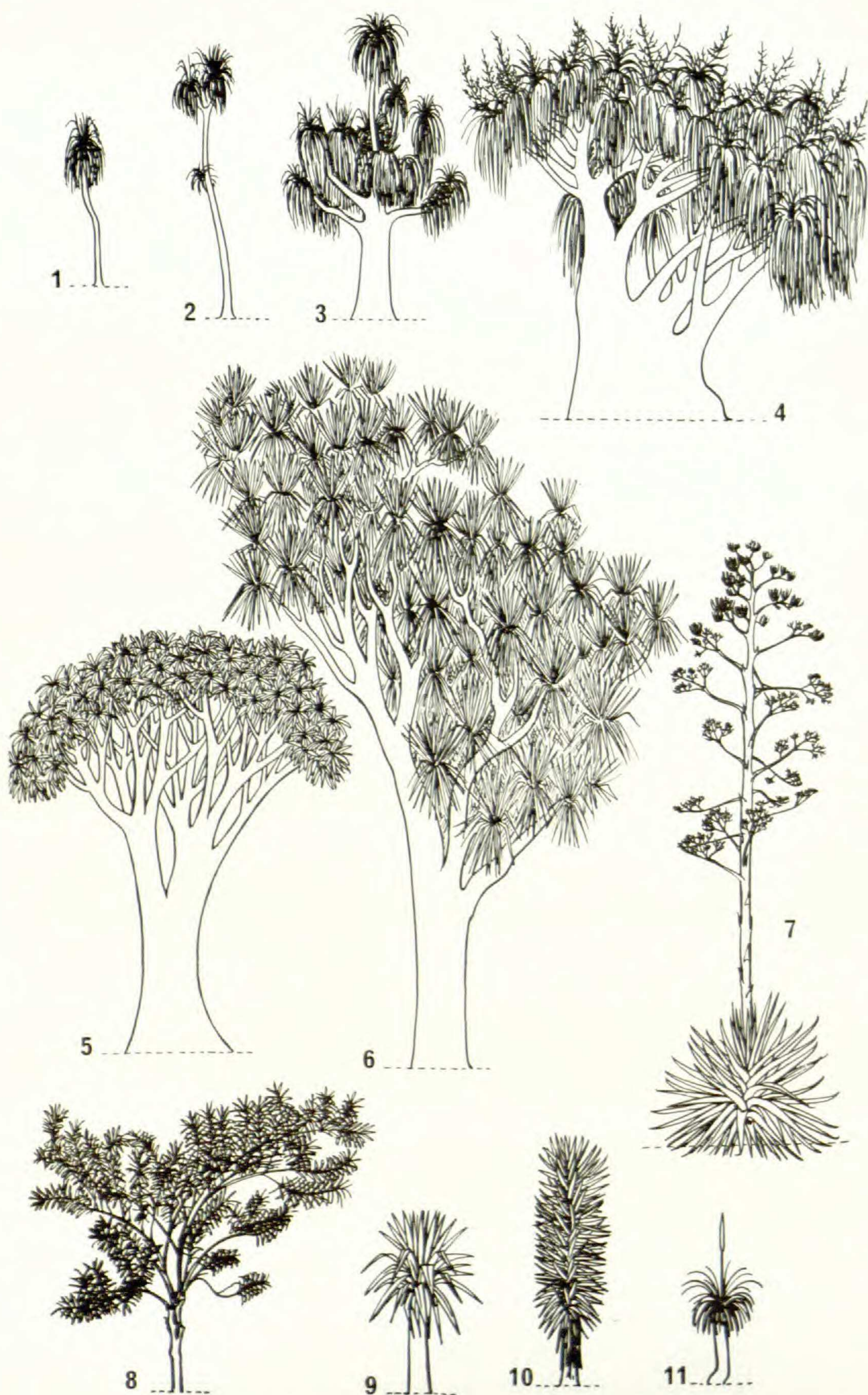
species, notably *A. bainesii* and *A. dichotoma*. *Agave* and *Furcraea* do not really fit a strict definition of a tree although some species achieve massive proportions. The same seems true of the Xanthorrhoeaceae although there is little information about their size, growth habit, and the extent of secondary tissue except in the work of Floresta (1902). The iridaceous genera are listed, although they are little more than shrubs, because secondary tissue is extensive and has been well described (e.g. Adamson, 1926; Scott & Brebner, 1893). On the other hand, we have omitted many monocotyledons which possess a limited amount of secondary growth but are otherwise essentially herbaceous. These include a number of genera in the Liliaceae, like *Aphyllanthes*, *Veratrum* and others in Hutchinson's Agavaceae. Fleshy rhizomes with secondary tissues, as in the Dioscoreaceae, are also disregarded. Vascular tissue which is by definition secondary may be quite common in other, unrelated, herbaceous monocotyledonous families [e.g. Bromeliaceae, Krauss (1948); Musaceae, Skutch (1932); Zingiberaceae, Chakraverti (1939)] where it seems to be associated with root insertion. However, before any major evolutionary significance can be attached to secondary cambial activity, we must attempt to understand it from a developmental point of view.

MORPHOLOGY

Growth habits (FIGS. 1-11). Growth form is quite diverse although it can be seen to depend on a common pattern of development. Leaves are linear, usually rigid, often thick and fleshy. They are rarely distinctly petiolate as in some smaller species of *Cordyline* and *Dracaena*. Axes are made up of short, often very congested internodes. In slow-growing plants this results in the characteristic terminal tufts of leaves or, if the main axis is very much shortened, in the basal rosette which characterizes the *Agave*-habit (FIG. 7). Branching is usually sparse; the reason for this is discussed below. In *Agave* and *Furcraea* the vegetative axis may be unbranched so that the plant is monocarpic. Otherwise the rosette in these plants is propagated by basal and usually stoloniferous suckers. Stoloniferous shoots are not usually present in other genera but they are common in herbaceous relatives (e.g. *Sansevieria*). The habit of most arborescent monocotyledons is quite tree-like, and some may even be mistaken for a dicotyledonous tree by a superficial observer, as noted by Wright (1901). However, some species of *Dracaena*, especially those in its segregate genus *Pleomele*, look more like shrubs with their much-branched crown and fine twigs (FIG. 8).

It is evident that shoot diameter on a single plant is not entirely dependent on the amount of secondary growth. In smaller and much branched species variation in crown diameter is considerable and seems related to the vigor of the shoot. Basal, erect shoots are thickest and most vigorous; distal horizontal shoots are narrow and least vigorous. We have noted a range in primary shoot diameter of 6 to 30 mm. in *Pleomele*.

Some of the simpler growth forms can be looked upon as juvenile stages



FIGS. 1-11. Growth habits in arborescent monocotyledons with secondary thickening (all to approximately same scale). FIGS. 1-4. *Beaucarnea recurvata*.

in the development of the larger forms, which are fixed permanently. Development of a large *Beaucarnea* (FIGS. 1-4), for example, begins with a rapidly growing main axis which remains unbranched for several years. Leaves may be long persistent so that they clothe the axis of quite tall specimens. Many species of *Yucca* do not develop much beyond this stage (FIG. 10). A link between the specialized rosette of *Agave* and this juvenile habit is provided by a number of species of both *Agave* and *Furcraea* with relatively tall stems (e.g. *F. longaeva* illustrated in Engler & Prantl (1930) p. 419). Otherwise, normal development of the tree form continues with branching, the loss of leaves from the older stem parts, thickening of the base of the stem, and development of a fissured bark. The evolutionary relation between ontogeny and phylogeny is suggested by *Cordyline* in New Zealand. *Cordyline indivisa* can be equated with the unbranched juvenile stage of *C. australis* (FIG. 9) and in turn the low rosette of *C. pumilio* with a younger stage still.

A disproportionate thickening of the base of the stem characterizes mature plants (FIGS. 4, 5, 13) and has probably led to some exaggerated statements about their longevity. Speculations about possible great age have particularly centered around *Dracaena draco*. The early literature about this is summarized in the paper of Wossidlo (1868). Perhaps the most famous individual tree in this respect was the specimen of *Dracaena draco* of Orotava on Teneriffe, described by Alexander von Humboldt (1850). Its historical record goes back to the fifteenth century. But estimates that it dated back to the period of the building of the pyramids (4,500 years) are probably exaggerations, especially in view of the known rate of growth of *Dracaena reflexa* (Wright, 1901). In 1799 the famous tree of Orotava had reached a height of about 70 feet and a circumference of 48 feet at the base of the trunk. A hurricane destroyed it in 1821. There is no certain method of telling the age of a specimen in the absence of planting data. A more meaningful time scale is given by a specimen of *Beaucarnea recurvata* (FIG. 13) in Fairchild Tropical Garden which is 25 feet high, 19 feet in circumference at a height of 2 feet and yet is known to be not more than 50 years old. Rates of growth otherwise appear not to have been determined for any of these plants.

Inflorescences are always terminal. On unbranched axes they are large and very conspicuous as in *Yucca* and Xanthorrhoeaceae (FIG. 11) and even on young specimens of *Beaucarnea*. They reach massive proportions in *Agave* and *Furcraea*. In the much-branched forms flowering is usually simultaneous on all or most distal shoots and renders the tree very conspicuous. In temperate species flowering is seasonal as in *Cordyline*

Plants of successive ages to show development of massive trunk. 1, Unbranched sapling 5-6 years old. 2-3, Early development of branch system in older stages. 4, Mature specimen in flower. Flowering begins in saplings of the size shown in FIG. 1. and with it is initiated branching. 5, *Aloë dichotoma*. 6, *Cordyline australis*. 7, *Agave* sp. 8, *Pleomele* (*Dracaena*) *reflexa*. 9, *Cordyline indivisa*. 10, *Yucca aloifolia*. 11, *Xanthorrhoea quadrangulata*.



FIG. 12. Specimens of *Cordyline australis*, growing in their natural habitat near Owhango, New Zealand.

FIG. 13. *Beaucarnea recurvata*, specimen about 50 years of age, at the Fairchild Tropical Garden in Miami, Florida.

FIG. 14. *Dracaena fragrans*. Outgrowth of branches from dormant axillary buds after decapitation.

FIG. 15. *Pleomele reflexa*. Outgrowth of branches from dormant axillary buds on the upper side of a leaning stem.

australis in New Zealand. Tropical and sub-tropical species may flower more than once each year. In general, however, there is little information about phenology and rates of growth of these plants.

Growth of axes seems to be continuous. At least it is not of a periodic

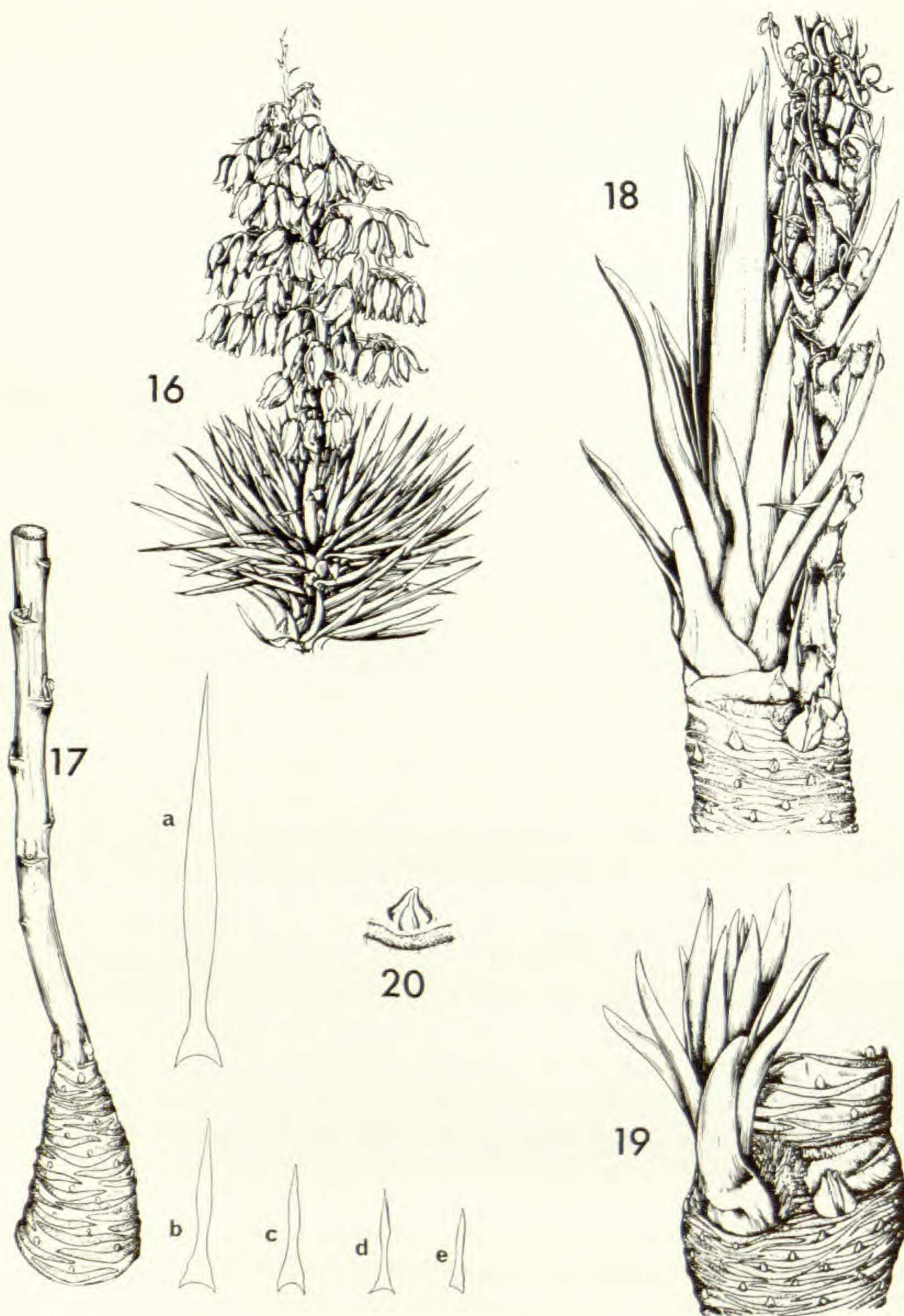
kind which involves resting buds protected by bud scales. Axes are always evergreen. Infrequent branching, which characterizes most monocotyledonous trees, is related to this continuous growth as will be suggested below.

Buds. In most groups each leaf subtends a minute bud (FIG. 17) which is strongly inhibited and very inconspicuous. It is either embedded in the stem tissue or enveloped by the prophyll (FIG. 20). Vegetative axillary buds are regularly present in *Dracaena* and related genera but their occurrence is less regular in *Aloë* (Schoute, 1903). Palms are in strong contrast because here the leaf axils in the mature vegetative phase of development are without vegetative buds (Tomlinson, 1964). However, there is no constant correlation between the presence of vegetative axillary buds and the development of secondary tissues. In Pandanaceae, with no secondary growth, axillary buds are present.

Sympodial branching below inflorescence (FIGS. 16–20). With the exception of the palms branching is normally sympodial in woody monocotyledons, regardless of whether they have secondary vascular tissue or not (Schoute, 1903, 1918). The sequence of events is quite obvious. The terminal shoot meristem is transformed from vegetative to reproductive, and a terminal inflorescence is produced (FIGS. 16, 17). This inflorescence eventually dies, and the inhibition of one or more buds in the axils of foliage leaves immediately below the terminal inflorescence is thus released (FIG. 18). If only one of these buds grows out it replaces the parent axis, pushing the inflorescence aside (FIG. 19). In this way sympodia are developed, segmented by the scars of pseudolateral, but originally terminal, inflorescences. Each unit of the sympodium is a lateral branch from the parent axis. When more than one lateral bud grows out, the sympodium forks and in this way a “dichotomy” may be simulated although the remains of the terminal inflorescence above the fork can always be found. Schoute (1903) described this pseudo-dichotomy in careful detail but his observations have been largely overlooked. For example one finds recent reports which refer to this type of branching as a “true dichotomy” in order to provide “evidence” for very fanciful evolutionary theories (e.g. Meeuse, 1961; 1965 and elsewhere).

Although the morphology of this sympodial branching is otherwise well understood, there has been no anatomical investigation of the way in which continuity of vascular tissue beneath branch and parent axis is developed. We shall consider this aspect in a later article.

Branching in the absence of flowering. Apical dominance of terminal over lateral buds is obviously very strong during normal growth of the axis. Since growth is seemingly continuous, no branches develop. Flowering and the ultimate death of the reproductive shoot releases apical dominance and enables one or more lateral buds to grow out. This happens at more or less regular intervals. In addition to this mechanism



FIGS. 16-20. Sympodial branching after flowering in *Yucca aloifolia*. 16, Habit of a flowering plant, $\times 1/10$. 17, Defoliated flowering stem to show the reduction in diameter throughout the transition from vegetative to inflorescence axis, $\times 1/3$, a-e showing the gradual reduction of leaf size, $\times 1/5$. 18, Outgrowing axillary bud has pushed the dead inflorescence to the right, $\times 1/3$. [Note that several axillary buds began to grow out but were later inhibited by the one which became dominant.] 19, A much later stage with the sympodial branch fully grown and the inflorescence weathered away (between two partially grown lateral buds), $\times 1/3$. 20, Dormant axillary bud, $\times 1$.

release of apical dominance may occur in other ways. One or more buds are usually released when a shoot is accidentally or experimentally decapitated (FIG. 14). Buds may also grow out of the upper side of the leaning stem in the absence of decapitation (FIG. 15). These phenomena may be explained according to familiar theories of the redistribution of growth regulators (Münch, 1938; Thimann, 1964). Similarly, release of buds at the base of old stems produces sucker shoots. It is likely that all these types of branching result from the same physiological cause.

PRIMARY VASCULAR STRUCTURE

The serious study of monocotyledonous anatomy began in the early nineteenth century and was largely stimulated by the theory of the "endogenous" growth as against the "exogenous" growth of dicotyledons. This theory seems to have originated with Daubenton (see Branner, 1884) and was elaborated by Desfontaines (1798). It owed much of its initial success to De Candolle (1813) who adopted it as a basis for distinguishing the two main classes of Angiosperms. The earliest work centered on arborescent forms, notably the palms, because as von Mohl emphasized, "the characters of the Monocotyledons are most clearly exhibited in them." The woody Liliiflorae, with secondary growth were given as much attention as monocotyledons without secondary growth. Attempts were made to equate these two types in developmental terms, but the resultant theorizing is now largely of historical interest. Investigations of this period are significant because they provided some reliable factual information, and also established the major taxa in which secondary tissue was to be found. Contributors of this period included Dupetit-Thouars (1809) and Mirbel (1809).

The theory of endogenous growth was effectively demolished by von Mohl (1824) when he described the overall course of bundles in the palm stem and indicated the regular way in which bundles cross over in a manner which could not be accounted for by endogenous growth. The process of demolition was completed by Meneghini (1836) and Mirbel (1843) who essentially confirmed von Mohl's observations. In a subsequent study of *Dracaena draco* Mirbel (1845) came to the conclusion that the growth of this plant was exogenous.

A paradox which has resulted from our modern understanding of vascular development in monocotyledons (e.g. Zimmermann & Tomlinson, 1968) is that we could easily reinstate, in a somewhat modified sense, the concept of "endogenous growth" of the primary vascular system of monocotyledons, and contrast it with the "exogenous growth" of dicotyledons, and the secondary vascular tissue of monocotyledons.

Von Mohl thought that the lower ends of vascular bundles in palms were reduced to narrow peripheral fibrous strands. We have referred to this basic error in detail elsewhere (Tomlinson & Zimmermann, 1966). He noted that the distribution of primary bundles in *Dracaena* was of the palm type and regarded the secondary bundles as the basipetal continua-

tion of the lower ends of the primary ones. Meneghini (1836) disputed this point with von Mohl who re-examined the matter in 1849. He was to refer to it once more (von Mohl, 1858) but the question was never really settled, as we now know the primary vascular anatomy had not been completely analyzed at the time and the explanations offered simply compounded existing errors. One of our first tasks in continuing this study will be to describe the primary vascular anatomy of *Dracaena* and show how it is indeed like a palm, but according to our modern understanding (Zimmermann & Tomlinson, 1969).

SECONDARY VASCULAR STRUCTURE (FIGS. 21, 22)

Information about the anatomy of secondary vascular tissue is available in a series of articles from Millardet (1865) and Wossidlo (1868) to Cheadle (1937). The secondary tissue consists of vascular bundles embedded in ground parenchyma. The original radial alignment of cambial derivatives is readily lost, except in stems with a high proportion of parenchyma to bundles. Cordemoy (1893) who was concerned with the function of this tissue noted that the ground parenchyma commonly contains calcium oxalate deposits in the form of raphides and other crystalline inclusions, frequently starch and sometimes oils. He further distinguished between stems in which the secondary ground tissue was lignified and thick-walled and those in which it was not. The latter situation is most characteristic of underground organs, as in rhizomes of Dioscoreaceae.

Individual vascular bundles are usually amphivasal, with a peripheral series of long overlapping tracheids surrounding a central phloem strand. The development of these tracheids in relation to other cells of the conducting strands will be discussed in further detail below. The xylem also includes short parenchyma cells. Phloem also includes short parenchyma cells and sieve-tube elements which have simple sieve plates on more or less transverse end walls. Russow (1882) concluded that these sieve tubes functioned indefinitely because the amount of callose in them did not change with the age of the bundle. In this presumed ability to function indefinitely these sieve tubes recall those of palms (Parthasarathy & Tomlinson, 1967). The bundles anastomose extensively, mostly in the tangential direction. Continuity with the primary vascular tissues is effected by short bridges which link with the leaf traces as described below.

Indistinct growth rings have been recorded by a number of observers (FIG. 23) (e.g. Floresta, 1902; Lindinger, 1909). Chamberlain (1921) was not the first to record this phenomenon, as he claimed. The rings are often more conspicuous to the naked eye than they are under the microscope and seem to be the result of a tendency for bundles to be arranged in tangential rows together with slight variation in cell size and the amount of wall thickening in successive layers. Whether growth rings are related to fluctuations in shoot growth or not is not known.

Formation of secondary vascular tissue (FIG. 21). Mirbel (1843)

recognized the essential features of the *Dracaena* cambium, as a meristematic zone which continually produces secondary vascular bundles. Later authors like Karsten (1847), Schacht (1852), and Nägeli (1858) were most concerned with theories about the equivalence of secondary vascular meristems in monocotyledons and dicotyledons, but the little information they produced was largely superseded by the more complete observations of later investigators.

The work of Röseler (1889) was the first detailed attempt to account for the process of division in the cambium and the way in which secondary vascular bundles differentiate from the derivatives. It was by no means the first of such investigations but it set a much higher standard than previous ones. It had become common knowledge, for example, that the tracheids in the secondary bundles are much longer than the cambial initials and their derivatives, whereas other elements of the bundle, like sieve-tube elements, phloem and xylem parenchyma are of the same length. Most early authorities assumed that the tracheids achieved their length by growth of a single derivative and that no cell fusion was involved. Krabbe (1886), for example, used these tracheids in *Dracaena* as an example in his work on sliding growth. Nevertheless these observations were disputed by a number of observers, notably by Kny (1886), who was of the opinion that no elongation of cambial derivatives was involved, but rather that the so-called tracheids were actually short vessels produced by the fusion of a longitudinal file of cells. The background to this controversy has been reviewed by Scott and Brebner (1893). Röseler (1889) re-instated the original concept on a firm basis by examining macerated material in which he demonstrated stages in the elongation of future tracheids. Another method he used, which involved counting the number of cells in transverse sections of the vascular bundle at different stages of development, proved to be less successful because, as Scott and Brebner emphasize, there is no fixed point at which counting could begin. Sliding growth evidently begins before cell division has ceased. It is also a matter of observation that the innermost tracheids at one level in any bundle are mature whereas outermost cells are still elongating or even dividing (FIG. 21). In addition the number of cells in a bundle varies and it is impossible to observe the same bundle at different stages of development.

The dispute was finally settled by Scott and Brebner themselves who confirmed Röseler's conclusions with various kinds of observations in spite of the fact that Scott (1889) himself had earlier supported Kny's opinion. They also suggested that the interpretation of other workers had resulted from a failure to distinguish carefully between developing tracheids and young sieve tubes in which nuclear breakdown simulates early stages in cell fusion. All subsequent investigators have found no cause to doubt Röseler's observations (cf. Cheadle, 1937).

Cambial division (FIG. 21). Most of our knowledge of the actual process of division in the cambial region is the result of a detailed study by Schoute (1902). He came to the conclusion that the meristem is at

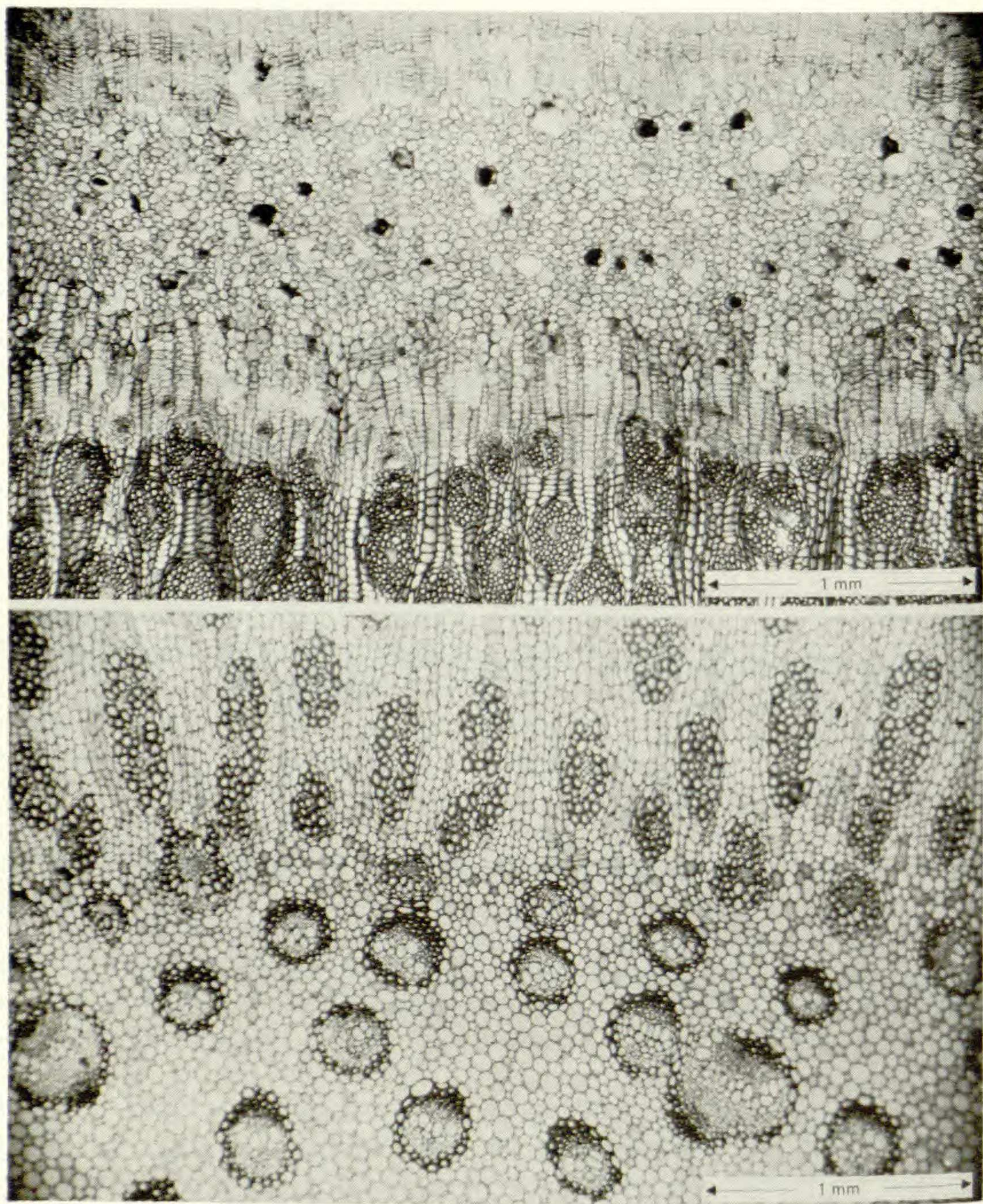


FIG. 21 (ABOVE). *Cordyline indivisa*, the mountain cabbage tree of New Zealand. Transverse section of stem at the periphery of the secondary tissue to show etagen cambium and stages in development of vascular bundles. A cork cambium, originating in the cortical parenchyma produces outer bark. (From Tomlinson & Zimmermann, 1967).

FIG. 22 (BELOW). *Dracaena hawaiiensis*. Transverse section showing the boundary between primary (collateral bundles at bottom of picture) and secondary tissue (amphivasal bundles amidst radially-seriated parenchyma at top of picture). (From Tomlinson & Zimmermann, 1967).

first tiered (Etagenmeristem) and involves a succession of tangential longitudinal divisions in parenchyma resulting in radially-seriated derivatives. The innermost derivatives become incorporated in the secondary tissue whereas divisions are repeated in outer derivatives. Some of the outer-

most derivatives may remain undivided and form a "secondary cortex," the extent of this tissue being determined by the vigor of the cambium according to Cordemoy. This type of activity may only be a temporary stage in development of the cambium and Schoute compared it with the early stages in the establishment of the interfascicular cambium in dicotyledons. Subsequently a true "initial" cambium, more like that of dicotyledons, is established in which divisions are said to be confined to a single series of initials. At this later stage derivatives are now added more consistently on the outside as the parenchymatous secondary cortex. In *Beaucarnea*, for example, Hausmann (1908) concluded that the same meristem was distally an etagen meristem, but proximally an initial meristem. Cheadle (1937) essentially concurred with these observations and added some comments on variation in shape of the cambial initials. He was the first to publish photographs of the cambium in tangential view, although tangential illustrations had been provided earlier, as in the drawings by Millardet (1865). It should be noted, however, that our understanding of divisions in this cambium is largely based on a study of the plane of insertion of new cell walls rather than by observation of nuclear divisions. In addition, in Schoute's account it is hard to distinguish theoretical inference from direct observation. It is clear that there is still a great deal to be learned about this monocotyledonous cambium from cytological studies. We must agree with Cheadle when he says "neither the exact location nor a convincing description of the cambial initials could be found in the literature."

Distribution of cambial activity in the tree. Shoot growth and cambial activity are correlated, but not in a very straightforward way, as our future discussion will reveal. Young, unbranched stems of *Dracaena draco* may have a slight obconical form which may be repeated in the distal branches of older trees. It is more usual, however, for the basal part of the main trunk to be much thicker than distal parts. This is of obvious adaptive significance as it makes for mechanical stability. This pronounced basal thickening is entirely due to secondary growth. The disproportionate bulbous expansion of the base of the stem to which it leads has already been described. We do not know what is responsible for the initiation of cambial activity in the primary shoot and how cambial activity is maintained. However, there is strong external evidence that distal branching and the outgrowth of new laterals is a stimulus to cambial activity below. In *Dracaena fragrans*, for example, we have observed that secondary vascular tissue is always present immediately below each new unit of the sympodium, and it is often discontinuous below so that the segmented appearance of the stem caused by sympodial growth is enhanced by a variation in stem thickness. A discontinuous distribution of secondary tissue in *Dracaena* roots as observed by Scott and Brebner may also be recalled. This situation will be discussed in detail in a later paper; it is of considerable functional significance. It is equally clear, however, that secondary thickening occurs in the absence of branching

as in seedling axes, although Dupetit-Thouars (1809) had initially suggested such a dependence between branching and secondary growth, a suggestion soon corrected (e.g. Wossidlo 1868, p. 25).

Although we have, as yet, little precise information about cambial activity in monocotyledons, the similarity of the phenomenon with that in conifers and dicotyledons is striking. Discontinuous cambial activity is known, for example, in very long roots of some dicotyledonous trees (Wilson, 1964). Another striking similarity is the asymmetric distribution of cambial activity in a leaning stem. Near Cape Sabal, in the Everglades National Park, the authors found a specimen of *Yucca aloifolia* which evidently had been thrown down by a hurricane a few years earlier. From the time of displacement the new shoot grew vertically again, but the displaced older part of stem remained in a leaning position. Transverse sections of the vertical part of the stem showed quite symmetrical arrangement of the secondary tissue, while on the leaning portion secondary growth had been quite asymmetric (diameter of primary stem 50 mm., radius of secondary tissue on upper side 8 mm., lower side 25 mm.).

On the other hand "reaction wood" has not been described for monocotyledons even in studies which have specifically been concerned with its distribution (Scurfield, 1964). This reflects the marked histological difference between monocotyledonous and dicotyledonous woods (Tomlinson & Zimmermann, 1967). Axes in these woody monocotyledons seem to be righted by re-orientation of the crown through unequal distribution of primary growth.

SECONDARY THICKENING IN ROOTS (FIGS. 24, 25)

It is known from the observations of many investigators (but see especially Lindinger, 1906) that in the roots of arborescent monocotyledons secondary thickening occurs only in *Dracaena*. However, from what is known about the method of insertion of adventitious roots in woody monocotyledons (and this knowledge is still based on the early account by Mangin (1882)) a limited amount of secondary thickening may occur in roots close to their insertion. This is nevertheless a matter for conjecture.

In *Dracaena*, all observers have noted that the secondary tissue in the root is identical in structure and origin with that in the stem. A major point of disagreement, however, has been the site of origin of the cambium which produces the tissue. Most early authors (e.g. Strasburger, 1884; Morot, 1885) recorded this as being the pericycle, although cambial activity could spread into the cortex via rupture of the endodermis. Others (e.g. Lindinger, 1906) recorded an exclusively cortical origin for the cambium. Scott and Brebner (1893) recorded both possibilities, together with a mixed condition where secondary growth began in the pericycle but then continued in a cambium formed in the cortex. In some instances all three conditions could be demonstrated in a single section (FIGS. 24, 25). They also made the very significant observation that secondary tissues are

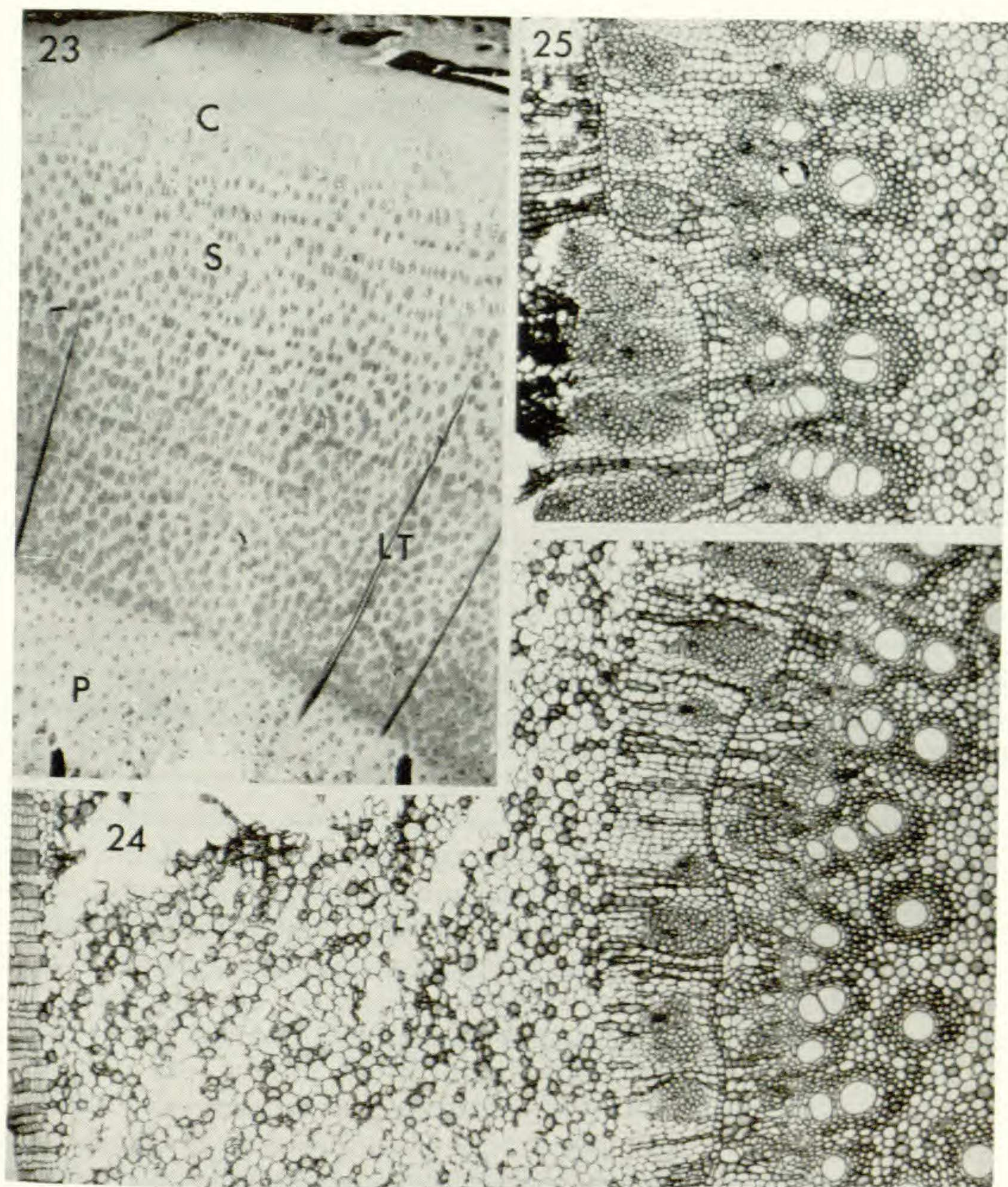


FIG. 23. *Yucca aloifolia*. Transverse section of stem at very low magnification, $\times 3.8$, showing some primary (P) and secondary (S) tissue. Growth rings are evident in the secondary tissue particularly if the illustration is viewed from a distance. Cambium at C. Leaf traces (LT) traversing stem radially.

FIGS. 24, 25. *Dracaena fragrans*, transverse section of root, $\times 33$. A small amount of secondary tissue is present. [Note the position of endodermis showing that cambial activity began in places inside it, in other places outside of it.]

always thickest in the region of insertion of lateral roots, and suggested that secondary thickening is initiated in this region.

It is quite obvious that the somewhat conflicting observations of different workers have a rational explanation in terms of growth and the factors which influence cambial development and activity. The problem has to be studied by following the origin and subsequent growth of adventitious roots in seedlings of different age, as Wright (1901) suggested. Wright

also made the observation that the cambium originates in the pericycle of the very short hypocotyl, thence spreading upward into the stem and downward into the root. Further observations of this kind are needed to establish a clear understanding of secondary growth in roots of *Dracaena*.

THE RELATION OF PRIMARY TO SECONDARY GROWTH

The earlier studies on growth and development of these monocotyledons were carried out at a time when the understanding of plant growth in general was at a very primitive stage. It was also inevitable that theories of plant growth were dominated by concepts derived from studies of dicotyledons, and some of the earliest interpretations of monocotyledonous growth made unfortunate comparisons between monocotyledons and dicotyledons. To this early period belong a series of studies concerned with the relation between the secondary "thickening ring" and the meristematic tissues of the shoot apex proper as in the investigations of Karsten (1847), Schacht (1852), Nägeli (1858) and Sanio (1863). It seems that these studies were based on examination of single sections cut in transverse and longitudinal planes and that no attempt was made to trace the distribution of developing vascular bundles and the 3-dimensional relation between primary and secondary growth. We will show in a later article that this kind of investigation is crucial to the understanding of this relation.

One of the features of arborescent monocotyledons which captured the interest of earlier workers was the apparent continuity between the secondary meristem and the meristematic tissues of the crown. Some authors considered these two meristems to be discontinuous (e.g. Scott & Brebner, 1893). This discontinuity is also implied by Millardet (1865) who gave measurements of the distance below the apex at which the secondary meristem could be first recognized. This varied from as little as 3 mm. in *Yucca aloifolia* to as much as 22 cm. in *Dracaena marginata*. On the other hand many authors regarded the two meristems as continuous (e.g. Wossidlo, 1868; Lindinger, 1908). Hausmann (1908) reviewed the extensive literature on this topic and himself supported the latter point of view, concluding in fact that the distinction between the two meristems was rather artificial. In a developmental sense this is true, because establishment and activity of secondary tissue is dependent upon growth of the primary meristem. Nevertheless, earlier authors have often adopted a very dogmatic point of view, largely in an effort to establish whether the secondary meristem originated in tissue which had completed its maturation or not, and was therefore, *by definition*, truly "secondary."

A similar dogmatic preoccupation which is also largely a semantic one, was with the level, in a radial direction, at which divisions which initiated the secondary meristem occurred. The problem was to decide whether there was a region in the monocotyledonous stem, to which the term "pericycle" could be given. This is entirely an artificial concept, since in most monocotyledonous stems, cortex and central cylinder each ends where the other begins. A true understanding of the development of that region

of the stem in dicotyledons for which the older term "pericycle" was devised has been forthcoming only in recent years (Blyth, 1958). The term pericycle has no application in monocotyledonous stems (Carano, 1910).

In terms of the overall distribution of the monocotyledonous cambium, one factual error does deserve comment. Röseler (1889) and apparently some earlier authors stated that the cambium does not extend into the leafy zone of the shoot. This is manifestly so untrue a generalization, whatever may have been the situation in the material on which it was based, that it is not surprising that it was soon corrected (e.g. by Corde-moy, 1894). The presence of functioning leaves, the traces of which must cross the cambium and secondary tissues, does raise interesting physiological and developmental questions to which we will return in a later article.

One reason for the conflicting reports on these topics which appears in the literature was that many authors failed to appreciate the variability in the time of appearance of the cambium and its vigor, which in turn seems largely to depend on the vigor of the shoot. We have already commented upon the variation in vigor expressed in the different diameters of shoots in one plant. This variation extends to the secondary cambium and may depend largely on the type of shoot. Seedling axes, for example, initially produce secondary tissue very actively. This activity declines on distal branches. Newly released buds, either below inflorescences or decapitated shoots, are dependent on an active production of secondary tissue in the early stages of growth in order to establish vascular continuity with the parent axis. In view of this variation it is not surprising that reports by early authors conflict, since they are probably based on comparison of shoots in different positions and of differing vigor.

COMPARATIVE INVESTIGATIONS

A few authors have been concerned with the relation between those monocotyledons with secondary growth and those without. Notable are Mangin (1882) and Petersen (1893). Chouard (1936) was concerned with the same topic, but his interpretations of monocotyledonous growth are not easy to comprehend. Petersen studied a number of monocotyledons which together represented a wide variety of families and growth forms. He came to the conclusion that in the group as a whole there was a continuous series with all intermediate steps, from those, like the orchids with no trace of a secondary meristem, via those in which one is briefly active, as in the Bromeliaceae, to the continually active cambium of *Dracaena* which permits unlimited growth.

Mangin (1882), on the other hand, was concerned with the way in which adventitious roots develop and establish vascular continuity with the conducting tissues of the parent axis. Adventitious roots arise in a meristematic region (*couche dictyogène*) between cortex and central cylinder. This meristem also gives rise to a plexus of vascular tissue (*réseau radicifère*) which connects conducting tissues of root and stem.

The extent of this plexus varies in different kinds of monocotyledons. Mangin considered that in some arborescent monocotyledons, like *Agave*, this meristematic region remains active throughout the life of the plant. In others, like *Dracaena* and *Yucca*, the root meristem is replaced by the secondary meristem. When more is known about the factors which stimulate and maintain an active cambium in monocotyledons it will be possible to approach the topic on a comparative base. Nevertheless Mangin's contribution to anatomical literature remains a notable one.

CONCLUSIONS

It is obvious from the previous pages that a reappraisal of this subject from first principles is needed. We hope to present in future articles the results of studies which to a large part resolve much of the conflicting literature. In particular we will describe the course and developmental pattern of the primary vascular bundles, the constructional relation between primary and secondary vascular bundles and demonstrate how the initiation and activity of the secondary meristem is dependent upon shoot growth. These will be related to growth of the shoot system as a whole.

LITERATURE CITED

- ADAMSON, R. S. 1926. On the anatomy of some shrubby Iridaceae. Trans. Roy. Soc. S. Afr. 13: 175-195.
- BLYTH, A. 1958. Origin of primary extraxylary stem fibers in dicotyledons. Univ. Calif. Publ. Bot. 30(2): 145-231. 23 pls.
- BRANNER, J. C. 1884. The course and growth of the fibro-vascular bundles in palms. Proc. Am. Philos. Soc. 21: 459-483.
- CANDOLLE, A. P. DE. 1813. Théorie élémentaire de la botanique. viii + 527 pp. Déterville, Paris.
- CARANO, E. 1910. Su le formazioni secondarie nel caule delle Monocotiledoni. Ann. Bot. Roma 8: 1-42.
- CHAMBERLAIN, C. J. 1921. Growth rings in a monocotyl. Bot. Gaz. 72: 293-304.
- CHAKRAVERTI, D. N. 1939. The occurrence of fugacious cambium in the rhizome of *Curcuma longa* Linnaeus. Philipp. Jour. Sci. 69: 191-195.
- CHEADLE, V. I. 1937. Secondary growth by means of a thickening ring in certain monocotyledons. Bot. Gaz. 98: 535-555.
- CHOUARD, P. 1936. La nature et le rôle des formations dites "secondaires" dans l'édification de la tige des Monocotylédones. Bull. Soc. Bot. Fr. 83: 819-836.
- CORDEMOY, H. J. DE. 1893. Sur le rôle des tissus secondaires à réserves des Monocotylédones arborescentes. Compt. Rend. Acad. Paris 117: 132-134.
- . 1894. Recherches sur les Monocotylédones à accroissement secondaire. pp. 108. 3 pls. Thesis. Paris.
- DESFONTAINES, R. L. 1798. Sur l'organisation des Monocotylédones, ou plantes à une feuille seminale. Mém. Acad. Sci. Paris. 1: 478-502.
- DUPETIT-THOUARS, L. M. A. 1809. Essais sur la végétation. 1. Sur l'accroissement en diamètre du tronc des *Dracaenas*, quoique Monocotylédones. pp. 10. Arthur Bertrand. Paris.

- ENGLER, A., & K. PRANTL. 1930. Die natürlichen Pflanzenfamilien. Ed. 2. 15a. Wilhelm Engelmann, Leipzig.
- FLORESTA, P. LA. 1902. Struttura ed accrescimento secondario del fusto di "Xanthorrhoea". Contr. Biol. Veg. Ist. Bot. Palermo 3(1): 191-208.
- HAUSMANN, E. 1908. Anatomische Untersuchungen an *Nolina recurvata* Hemsl. Beih. Bot. Centralbl. 23(2): 43-80.
- HUMBOLDT, F. H. A. VON. 1850. Views of nature, or contemplations on the sublime phenomenon of creation (English ed.). xiv + 452 pp. Henry G. Bohn. London.
- HUTCHINSON, J. 1959. The families of flowering plants. Vol. II. Monocotyledons. ed. 2. Clarendon Press. Oxford.
- KARSTEN, H. 1847. Die Vegetationsorgane der Palmen. Abh. Akad. Wiss. Berlin 1847: 73-236.
- KNY, L. 1886. Ein Beitrag zur Entwicklungsgeschichte der 'Tracheiden'. Ber. Deutsch. Bot. Ges. 4: 267-276.
- KRABBE, H. G. 1886. Das gleitende Wachstum bei der Gewebebildung der Gefäßpflanzen. vii + 100 pp. 7 pls. Gebrüder Borntraeger. Berlin. (See D. H. SCOTT in Ann. Bot. (Lond.) 2: 127-136. 1888.)
- KRAUSS, B. H. 1948. Anatomy of the vegetative organs of the pineapple, *Ananas comosus* (L.) Merr. I. Introduction, organography, the stem and the lateral branch or axillary buds. Bot. Gaz. 110: 159-217.
- LINDINGER, L. 1906. Zur Anatomie und Biologie der Monokotylenwurzel. Beih. Bot. Centralbl. 19: 321-358.
- . 1908. Die Struktur von *Aloë dichotoma* L., mit anschliessenden allgemeinen Betrachtungen. Beih. Bot. Centralbl. 24(1): 211-253.
- . 1909. Jahresringe bei den Monokotylen der Drachenbaumform. Naturw. Wochenschr. Jena. N.F. 8: 491-494.
- MANGIN, L. 1882. Origine et insertion des racines adventives et modifications corrélatives de la tige chez les monocotylédones. Ann. Sci. Nat. Bot. 14: 216-363.
- MEEUSE, A. D. J. 1961. The Pentoxylales and the origin of the Monocotyledons. Proc. Nederl. Akad. Wet. C. 64: 543-559.
- . 1965. Angiosperms — past and present. In: Advancing Frontiers of Plant Sciences 2: pp. 228.
- MENEGHINI, G. 1836. Ricerche sulla struttura del caule nelle piante Monocotiledoni. 110 pp. 10 pls. Minerva, Padua.
- MILLARDET, A. 1865. Sur l'anatomie et le développement du corps ligneux dans les genres *Yucca* et *Dracaena*. Mém. Soc. Sci. Nat. Cherbourg 11: 1-24.
- MIRBEL, C. F. B. DE. 1809. Nouvelles recherches sur les caractères anatomiques et physiologiques qui distinguent les plantes monocotylédones des plantes dicotylédones. Ann. Mus. Hist. Nat. Paris 13: 54-86.
- . 1843. Recherches anatomiques et physiologiques sur quelques végétaux monocotylés. Ann. Sci. Nat. Bot. II. 20: 5-31.
- . 1845. Suites des recherches anatomiques et physiologiques sur quelques végétaux monocotylés. Ann. Sci. Nat. Bot. III. 3: 321-337.
- MOHL, H. VON. 1824. De palmarum structura. In: K. F. P. VON MARTIUS, Historia Naturalis Palmarum 1: pp. I-LII. 16 pls.
- . 1849. On the structure of the palm stem. Rep. Roy. Soc. 1849: 1-92.
- . 1858. Ueber die Cambiumschicht des Stammes der Phanerogamen und ihr Verhältniss zum Dickenwachsthum desselben. Bot. Zeit. 16: 185-190, 193-198.

- MOROT, L. 1885. Recherches sur le péricycle. *Ann. Sci. Nat. Bot.* VI. 20: 217–309.
- MÜNCH, E. 1938. Untersuchungen über die Harmonie der Baumgestalt. *Jahrb. Wiss. Bot.* 86: 581–673.
- NÄGELI, C. 1858. Ueber das Wachsthum des Stammes und der Wurzel bei den Gefäßpflanzen. *Beitr. Wiss. Bot.* Heft 1. pp. 1–156. *Pls.* 1–19.
- PARTHASARATHY, M. V., & P. B. TOMLINSON. 1967. Anatomical features of metaphloem in stems of *Sabal*, *Cocos* and two other palms. *Am. Jour. Bot.* 54: 1143–1151.
- PETERSEN, O. G. 1893. Bemaerkninger om den monokotyledone staengels Tykkelsevaext anatomiske Regioner. *Bot. Tidsskr.* 18: 112–124.
- RÖSELER, P. 1889. Das Dickenwachsthum und die Entwicklungsgeschichte der secundären Gefäßbündel bei den baumartigen Lilien. *Jahrb. Wiss. Bot.* 20: 292–348.
- RUSSOW, E. 1882. Ueber den Bau und die Entwicklung der Siebröhren und Bau und Entwicklung der secundären Rinde der Dicotylen und Gymnospermen. *Sitzungsber. Naturforsch. Ges. Univ. Dorpat.* 6: 257–327.
- SANIO, C. 1863. Vergleichende Untersuchungen über die Zusammensetzung des Holzkörpers. *Bot. Zeit.* 21: 357–363; 367–375; 377–385; 389–399; 401–412.
- SCHACHT, H. 1852. Die Pflanzenzelle. Berlin (original not seen).
- SCHOUTE, J. C. 1902. Über Zellteilungsvorgänge im Cambium. *Verh. Akad. Wet. Amsterdam. Afd. Natuurk. sec. 2.* 9: 1–59.
- . 1903. Die Stammesbildung der Monokotylen. *Flora [Jena]* 92: 32–48.
- . 1918. Über die Verästelung bei monokotylen Bäumen. III. Die Verästelung einiger baumartigen Liliaceen. *Rec. Trav. Bot. Néerl.* 15: 264–335.
- SCOTT, D. H. 1889. On some recent progress in our knowledge of the anatomy of plants. *Ann. Bot. (Lond.)* 4: 147–161.
- & G. BREBNER. 1893. On the secondary tissues in certain monocotyledons. *Ann. Bot. (Lond.)* 7: 21–61.
- SCURFIELD, G. 1964. The nature of reaction wood. IX. Anomalous cases of reaction anatomy. *Austral. Jour. Bot.* 12: 173–184.
- SKUTCH, A. F. 1932. Anatomy of the axis of banana. *Bot. Gaz.* 93: 233–258.
- STRASBURGER, E. 1884. *Das botanische Practicum.* ed. 1. xxxvi + 664 pp. Gustav Fischer. Jena.
- THIMANN, K. V. 1964. (See the discussion following the paper by A. B. Wardrop, p. 451.) *In: The formation of wood in forest trees*, M. H. ZIMMERMANN, ed., Academic Press, New York.
- TOMLINSON, P. B. 1964. Stem structure in arborescent monocotyledons. *In: M. H. ZIMMERMANN, ed. The formation of wood in forest trees.* pp. 65–86. Academic Press, New York.
- & M. H. ZIMMERMANN. 1966. Vascular bundles in palm stems — their bibliographic evolution. *Proc. Am. Philos. Soc.* 110: 174–181.
- & ———. 1967. The “wood” of monocotyledons. *Bull. Int. Assoc. Wood Anatomists.* 1967(2): 4–24.
- TRELEASE, W. 1902. The Yuccae. *Ann. Rep. Missouri Bot. Gard.* 13: pp. 133. *Pls.* 99.
- WILSON, B. F. 1964. Structure and growth of woody roots of *Acer rubrum* L. *Harvard Forest Papers* 11: pp. 14.
- WOSSIDLO, P. 1868. Ueber Wachsthum und Structur der Drachenbäume. *Jahrb. Realsch. Zwinger, Breslau* 1868: 1–32.

- WRIGHT, H. 1901. Observations on *Dracaena reflexa* Lam. Ann. Roy. Bot. Gard. Peradeniya 1: 165-172.
- ZIMMERMANN, M. H., & P. B. TOMLINSON. 1968. Vascular construction and development in the aerial stem of *Prionium* (Juncaceae). Am. Jour. Bot. 55: 1100-1109.
- & ———. 1969. The vascular system in the axis of *Dracaena fragrans* (Agavaceae), I. Distribution and development of primary strands. Jour. Arnold Arb. 50: in the press.

[P.B.T.]

FAIRCHILD TROPICAL GARDEN
10901 OLD CUTLER ROAD
MIAMI, FLORIDA 33156

[M.H.Z.]

HARVARD UNIVERSITY
CABOT FOUNDATION
PETERSHAM
MASSACHUSETTS 01366

ASPECTS OF REPRODUCTION IN SAURAUIA

DJAJA D. SOEJARTO¹

THE GENUS *Saurauia* is a widespread tropical member of the Actinidiaceae with representatives in both the Old and the New World. The American range of distribution extends from Central Mexico to southern Bolivia, through Andean South America. According to a recent study by Hunter (1966), 22 species occur in Mexico and Central America, and my present study indicates that 49 species are represented in South America. The genus is not represented in the West Indies, and there are no records of its occurrence in the Guianas or Brazil.

During the course of field work in southern Colombia in 1965, I observed that some individuals of *Saurauia tomentosa* (H.B.K.) Sprengel have flowers with sessile stigmas, in contrast to the flowers with long styles (5–7 mm.) of individuals commonly held to be characteristic of the species. Later herbarium studies indicated that several other South American species are similar to *S. tomentosa* in this respect.

To be certain that such a phenomenon had not previously been described in *Saurauia*, I have searched the literature and found that nothing conclusive has ever been published. There are several references, however, to the reproductive system of *Saurauia*. Gilg (1895) and Gilg and Werdermann (1925) described the flowers of *Saurauia* as hermaphroditic to polygamo-dioecious. Brown (1935), who observed the flowering pattern of *S. subspinoso* Anthony, an Asiatic species, noted that the ovary development in this species lags behind the development of the anthers by about five days, suggesting that cross-pollination may be dominant. Hunter (1966) mentioned that some species in Mexico and Central America have flowers with "aborted" pistils. Killip (Jour. Wash. Acad. Sci. 16: 570. 1926) referred to the flowers of *S. micayensis* Killip as unisexual, while Benoist (Bull. Soc. Bot. France 80: 334. 1933) described the flowers of his *S. hypomalla* as staminate.

A few field workers have noted the existence of "male" and "female" plants in some species of *Saurauia*. Lorenzo Uribe Uribe, for example, noted the peculiarity in *S. isoxanthotricha* Busc. (L. Uribe U.'s collection number 4802): "Este pie, que crecía cerca a mí No. 4801, no tenía sino flores femeninas." (This tree, which grew close to my No. 4801, had only female flowers.)

The flowers of *Saurauia* are borne in a thyrsiform inflorescence, consisting of a peduncle, rachis, and axillary scorpioid cymes arising in a spiral pattern. Each cyme is borne in the axil of a bract. The flowers are

¹ The author is currently engaged in the revision of the South American species of *Saurauia*.

actinomorphic, pedicellate, each subtended by a bract and two lateral bracteoles; basically, the flowers are pentamerous and are usually described as bisexual or hermaphroditic. To the best of my knowledge, there is no true "male" or "female" plant; in other words, there is no true sexual dioecism in *Saurauia*.

The observations discussed in this paper were made to obtain more conclusive evidence about the reproductive system and its operations, and to suggest the implications for evolution in the South American species of *Saurauia*. This paper is the basis for more detailed studies on the breeding systems of the group which are in progress.

MATERIALS AND METHODS

The present investigation has been based primarily upon data obtained from herbarium specimens. Initially, the work consisted simply of sorting specimens with reproductive parts into long- and short-(obsolete-) styled groups. The next step was examination of the pollen grains (their morphology, size, and fertility) of individuals in each of the two groups. Pollen fertility count was obtained either from open flowers or from mature flower buds. The best results were obtained by boiling the flowers or flower buds (sufficiently mature) to obtain the anthers for maceration. Boiling restores the dried material to a natural texture, which makes dissection and measurement of the floral parts more accurate. The pollen grains were mounted in glycerine jelly and stained with cotton blue dissolved in water. All pollen fertility counts reported here were obtained by using a Wild M20 phase contrast microscope, with bright-field illumination with or without a green filter. Percentage numbers were based upon a count of between 100 and 500 pollen grains on a single preparation. From two to five samples were prepared from one individual.

Stamen counts were made for taxonomic purposes. More important to this study, however, was to ascertain whether or not stamen number has any significant relation to floral dimorphism. All counts were made by boiling the (mature) flower buds, since counts based upon open flowers may be inaccurate, as some stamens may have aborted or others may have been broken and fallen during the process of drying and handling.

Measurements of style length were made mainly from open flowers and/or fruits, since the styles are persistent in *Saurauia*. Style length is not reduced much by drying, so boiling was only occasionally necessary. When neither open flowers nor fruits were available, measurement was made from the mature flower buds. This is a valid and reliable substitute, as will be obvious from the following discussions.

OBSERVATIONS

Analysis of data. I have examined all species from South America for my taxonomic revision, but, due to lack of data, only species with sufficient representation are included here for discussion. These are *Sau-*